

MADAGASCAR FISH-EAGLE PREY PREFERENCE AND FORAGING SUCCESS

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ABSTRACT.—We investigated Madagascar Fish-Eagle (*Haliaeetus vociferoides*) foraging ecology to determine prey preference and the effect of fish abundance on fish-eagle foraging rates and foraging success. We observed fish-eagle foraging behavior at nine lakes in western Madagascar from May to August 1996. We sampled the fish population at each lake using gill nets and recorded fish weights and species. Introduced tilapia, *Oreochromis* spp. and *Tilapia* spp., made up the majority of both the gill net (66.3%) and fish-eagle catch (64.7%) in similar proportion, suggesting that the fish-eagle is an opportunistic predator. Consequently, replacement of native fish species by exotics probably has not been detrimental to the island's fish-eagle population. Male fish-eagle foraging success was positively correlated ($P < 0.001$) with number of fish species, suggesting that fish species diversity may affect fish-eagle foraging effectiveness. Received 24 July 1997, accepted 2 Nov. 1998.

Prey availability influences breeding area selection (Swenson et al. 1986), breeding density (Dzus and Gerrard 1989), reproductive success (Grubb 1995), and date of breeding (Hansen 1987) in Bald Eagles (*Haliaeetus leucocephalus*) and productivity in White-tailed Eagles (*Haliaeetus albicilla*; Helander 1985). It also affects distribution and density of Bald Eagles at wintering sites (Griffin and Baskett 1985, Sabine and Klimstra 1985, Keister et al. 1987, Hunt et al. 1992b) and migratory stopovers (Fraser et al. 1985, Bennetts and McClelland 1991).

Although prey availability is clearly important to *Haliaeetus* eagles, there has been little research aimed at quantitatively determining prey abundance and its effects on prey selection, foraging rates, and foraging success in the genus. Steenhof (1976), Mersmann (1989), and Hunt and coworkers (1992a) used gill nets to inventory relative fish abundance and determined that the most frequently netted fish species made up the greatest proportion of the Bald Eagle's diet. Wintering Bald Eagles in New Mexico fed most frequently on big game carrion when it was the most abun-

dant prey source (Grubb 1984). There is a positive relationship between prey abundance and foraging success of wintering Bald Eagles both between locations (Stalmaster and Plettner 1992) and between years (Brown 1993). Knight and Knight (1983) found a negative correlation between search time and relative prey abundance of Bald Eagles wintering in Washington, but Mersmann (1989) did not find a correlation between Bald Eagle foraging rates and gill net catch rates on the northern Chesapeake Bay.

Langrand and Meyburg (1989) and Razafindramanana (1995) have documented fish species eaten by Madagascar Fish-Eagles (*Haliaeetus vociferoides*), but there has been no previous attempt to quantitatively assess the eagle's diet. The objectives of this study were (1) to describe the diet and foraging behavior of the Madagascar Fish-Eagle at lakes in western Madagascar, (2) to determine fish-eagle prey preference, and (3) to determine whether fish-eagle foraging rates and foraging success are dependent on prey abundance.

STUDY AREA AND METHODS

We observed Madagascar Fish-Eagle foraging ecology from 22 May to 4 August 1996 at nine lakes in the Tsiribihina, Manambolo, and Beboka river drainages between the Bongolava escarpment and the Mozambique Channel in western Madagascar (Table 1). We selected lakes that we felt would offer the best conditions for viewing eagles throughout the day from among 32 lakes with resident Madagascar Fish-Eagle pairs that we studied in 1995 (Berkelman 1997).

We observed fish-eagle foraging behavior throughout daylight hours from 06:00 to 18:00 (GMT + 3 h) for six or seven days at each lake. We recorded both

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TABLE 1. Lakes included in Madagascar fish-eagle foraging ecology study in western Madagascar, May–August, 1996.

Lake	Coordinates	Dates observed
Ambereny	18° 55' S, 44° 23' E	22–28 May
Bejjo	19° 13' S, 44° 32' E	30 May–5 June
Ankazomena	19° 42' S, 45° 23' E	8–15 June
Asonjo	19° 50' S, 45° 26' E	16–23 June
Ampamandrika	19° 46' S, 44° 34' E	27 June–3 July
Befotaka	19° 1' S, 44° 24' E	7–12, 20 July
Masama	18° 50' S, 44° 27' E	13–19 July
Bevoay	19° 9' S, 44° 24' E	22–28 July
Tsiandrora	18° 58' S, 44° 38' E	30 July–4 August

observer-time, the number of hours spent observing eagles, and eagle-time, the product of observer-time and the number of eagles observed during each hour, for each lake. At the three lakes that had more than one resident fish-eagle pair, we randomly selected one of the pairs for observation during the period. We watched from an inflatable kayak or from the shore using 10 × 50 binoculars and a 15–45 × spotting scope on a rifle mount. We concentrated on the resident eagle pair while also noting the behavior of any other eagles that we could see, including immatures and other adults that were associated with the resident pair. We distinguished adult fish-eagle sexes by the smaller size and higher pitched vocalizations of the males. We distinguished adults from immatures by their vocalizations and by the completely white plumage on the tails and the faces of the adults (Langrand and Meyburg 1989).

We recorded prey searches when eagles flew low over the water looking down (Stalmaster and Plettner 1992) and kills when they picked up a fish from the water. We also noted instances of fish-eagles scavenging dead fish from the shoreline or pirating fish from Black Kites (*Milvus migrans*). We identified fish to species whenever possible. If we could not identify the fish while the eagle was in flight, we looked for prey remains on the ground beneath the eagle's feeding perch.

We set two monofilament gill nets for 3 h at each lake starting at 06:00–06:15. The gill nets had a foam core float rope and a lead core bottom rope, were 0.91 m deep by 45.7 m long, and were divided into three 15.2 m panels of 2.5, 3.8, and 5.1 cm mesh size. We attached floats to the first net and set it parallel to the shore in water about 0.9 m deep. We set the second net on the bottom, parallel to the shore, in water about 1.8 m deep. Thus, we sampled fish from among the first and second 0.9 m of the water column. If the lake was less than 1.8 m deep, we set the second net in the deepest water within 200 m of where we had set the first net. We placed nets adjacent to the nest or, where we did not find a nest ($n = 1$), adjacent to a frequently used perch. We believed that these sites were representative of fish-eagle foraging areas because we ob-

served the eagles forage most frequently within 300 m of the nest at eight of the nine lakes.

We identified each fish caught in the gill nets using keys (Arnoult 1959, Kiener 1963, Glaw and Vences 1994) and weighed it to the nearest g and measured total fish length to the nearest cm. We combined the data for the three days that we sampled each lake (nine hours total) and calculated total number of fish caught, total weight (kg) of fish catch, average fish weight (g), and number of species. We did not include fish that weighed over 1.5 kg in these calculations because we did not see fish-eagles capture larger fish.

We conducted the χ^2 test of equal proportions to determine if fish-eagle use of fish species was different from expected use based on gill net samples using SAS on an IBM compatible computer (PROC FREQ, SAS Institute Inc. 1990). We excluded unidentified prey from this analysis. After finding a significant ($P < 0.05$) overall difference, we tested the hypothesis of no difference between use and availability of each fish species, following Marcum's and Loftsgaarden's (1980) technique. We calculated Spearman correlation coefficients between fish-eagle foraging variables and fish variables (PROC CORR, SAS Institute Inc. 1990). For all analyses, we used an overall confidence level of $\alpha = 0.05$ and a confidence level of α/k , where k was the number of significance values calculated, following the Bonferroni approach (Miller 1966).

RESULTS

Foraging behavior.—There were extra adult Madagascar Fish-Eagles associated with three pairs and immatures with another three of the nine resident pairs that we studied. Altogether, we observed 11 adult males, 10 adult females, and 3 immatures.

Hunting methods were similar to those used by other sea eagles (Brown 1980, Love 1983, Stalmaster 1987). The fish-eagles we observed hunted from perches and either stooped directly from a perch or searched low over the water, generally returning to perch within 5

TABLE 2. Male Madagascar Fish-Eagle foraging at nine lakes in western Madagascar, May–August, 1996.

Variable	\bar{x} ($n = 11$)	SE
Searches	36.7	8.0
Kills	5.9	1.7
Searches/hour/eagle	0.68	0.15
Kills/hour/eagle	0.10	0.03
Kills/search	0.16	0.04

min of leaving. When striking, the eagles entered the water feet first at a low angle and only took fish that were at or just below the surface.

We watched eagles for 669.5 h observer-time and 1030.98 h eagle-time, including 490.25 h (47.6%) male eagle-time, 526.0 h (51.0%) female eagle-time, and 14.73 h (1.4%) immature eagle-time. We recorded 67 occurrences of eagles obtaining fish, including 60 (89.6%) occasions when they captured fish in open water, 3 (4.4%) when they scavenged dead fish from the shoreline, and 4 (6.0%) when they stole fish from Black Kites. We also recorded 32 occurrences of eagles eating fish or delivering fish to their mates when we did not see an eagle obtain the fish. On one occasion we observed an eagle eating a domestic duckling (*Anas* sp.). We did not see the eagle capture the duckling, but the local people claimed that the same eagle pair had killed domestic ducklings and turkey (*Meleagris* sp.) poults at the same lake on several occasions in 1996.

Of the 67 occasions when we saw eagles obtain fish, the eagles were adult males on 53 (79.1%) occasions, adult females on 13 (19.4%), and an immature on 1 (1.5%) occasion. Nine (69.2%) of 13 adult females that we saw capture fish were not nesting at the time. The other four (31.8%) were incubating eggs. All 32 occasions on which we saw eagles eating or delivering fish but did not see them catch the fish involved adult male eagles. All four instances of piracy from kites occurred at the same lake and involved two cooperating adult male eagles associated with the same territory. In each case, the eagles harassed a kite until it dropped its fish, which one of the eagles then retrieved.

Foraging rates and fish abundance.—Male

TABLE 3. Number of fish, total fish weight, average fish weight, and number of fish species caught in gill nets at nine lakes occupied by Madagascar Fish-Eagles in western Madagascar, May–August, 1996.

Variable	\bar{x}	SE	Range
Number of fish	30.1	7.3	4–66
Total weight, kg	4.6	1.6	0.2–15.9
Average weight, g	139.0	23.7	55.3–269.3
Number of species	3.9	0.4	2–6

fish-eagle kills/search was positively correlated with number of fish species caught in gill nets ($\rho = 0.909$, $P < 0.001$). There were no other significant correlations between fish-eagle foraging rates (Table 2) and fish variables (Table 3). We only analyzed male foraging because we rarely saw females forage.

The Madagascar Fish-Eagle search rate peaked in the early morning and again, at a higher level, in the early afternoon (Fig. 1A). Foraging success, expressed as the proportion of prey searches that resulted in kills, was highest before 10:00 and after 16:00 but lower between these times (Fig. 1B).

Dietary preference.—Of the 99 observed occurrences of fish-eagles capturing, carrying, or eating fish, we were able to identify 68 (68.7%) either to species or to a closely related group of species (Table 4). We were unable to identify eagle-caught tilapia to species or to distinguish between the closely related *Oreochromis* and *Tilapia* genera. In our gill net samples, we caught 271 fish of 12 species, including four species of tilapia and eight other species. The total weight of the catch at all nine lakes was 41.1 kg.

We combined all native fish species into a single group because our catches of each species were too small to analyze separately (Table 4). The proportions of fish species differed significantly between the fish-eagle catch and the gill net catch ($\chi^2 = 41.97$, $df = 4$, $P = 0.001$). The 95% confidence limits for the difference between the proportion used and the proportion available suggested that fish-eagles catch *Ophicephalus striatus* in greater proportion, *Cyprinus carpio* in lesser proportion, and tilapia, *Heterotis niloticus*, and native species in equal proportion to their relative abundance.

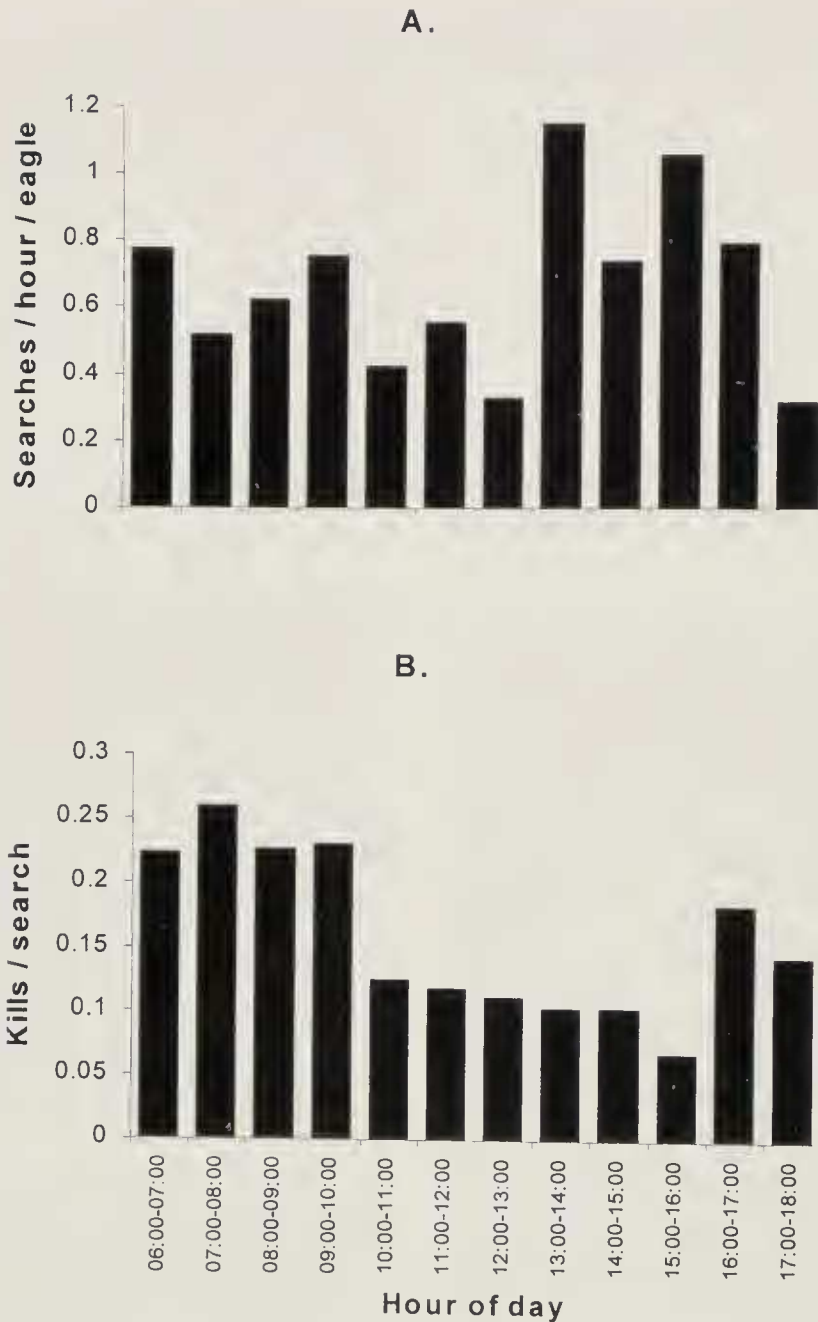


FIG. 1. Madagascar Fish-Eagle prey searches per hour per eagle (A) and prey searches resulting in kills (B) by time of day at nine lakes in western Madagascar, May–August, 1996.

DISCUSSION

Foraging behavior.—Our observation that 4.4% of fish taken by Madagascar Fish-Eagles were scavenged was lower than scavenging rates that Mersmann (1989) and Brown (1993) reported for Bald Eagles (25% and 7.7%, respectively) but comparable to the 4% reported by Stalmaster and Plettner (1992). We did not see fish-eagles take floating dead fish from the surface in open water, but it is possible that some of the fish that we observed eagles catch from a distance were dead fish floating below the water surface.

We are unaware of previous reports of pi-

racy or capture of avian prey by the Madagascar Fish-Eagle. It is unclear why we observed four instances of piracy at one of the lakes and none at the other eight lakes. We saw numerous other fish-eating birds at all the lakes, including Black Kites, herons, storks, anhingas, and cormorants.

Although we observed adult male eagles incubating eggs and tending nestlings, it appears that the male does most of the foraging for the pair, at least during early nesting. The four instances in which we observed incubating females catch fish occurred near the nest when males were not present. The most advanced

TABLE 4. Fish caught (number and % of total) and number of lakes where fish were caught (out of nine) by Madagascar Fish-Eagles and in gill nets in western Madagascar, May–August, 1996.

Fish species ^a , family	Fish-eagle catch			Gill net catch		
	No. of fish	% of fish	No. of lakes	No. of fish	% of fish	No. of lakes ^b
Exotic						
<i>Tilapia</i> ^c , Cichlidae	44	64.7	9	183	67.5	9
<i>Heterotis niloticus</i> , Osteoglossidae	7	10.3	3	17	6.3	3
<i>Cyprinus carpio</i> , Cyprinidae	2	2.9	2	33	12.2	1 (2)
<i>Ophicephalus striatus</i> , Channidae	10	14.7	6	1	0.4	1 (6)
Native						
<i>Megalops cyprinoides</i> , Megalopidae	2	2.9	2	18	6.6	6 (1)
<i>Arius madagascariensis</i> , Ariidae	3	4.4	3	14	5.2	5
<i>Glossogobius giurii</i> , Gobiidae	0	0	0	2	0.7	1
<i>Ambassis gymnocephalus</i> , Ambassidae	0	0	0	2	0.7	1
<i>Scatophagus tetracanthus</i> , Scatophagidae	0	0	0	1	0.4	1
TOTAL	68	100		271	100	

^a Unidentified fish that fish-eagles caught ($n = 31$) were excluded.

^b Number in parentheses represents additional lakes where each fish species was known to be present either from 1995 gill net sampling or from fish catches of local fishermen.

^c *Tilapia* species included in order of decreasing gill net catch: *Oreochromis macrochir*, *Tilapia zillii*, *O. mossambicus*, and *O. niloticus*.

nesting attempt we observed had a 2–3 week old downy chick, so we were unable to document whether female fish-eagle foraging rates change as nesting progresses.

Foraging rates and fish abundance.—The strong positive correlation between fish-eagle kills/search and number of fish species may indicate that the eagles forage most effectively at lakes that have the highest fish species diversity. In a previous study, Berkelman (1997) found that fish species diversity, along with shoreline perch density, was one of the best predictors of fish-eagle lake use, lending further support to the importance of fish species diversity. However, the strength of the correlation between foraging success and fish species diversity may be related to the low range of variability in number of fish species caught (2 to 6) at lakes in this study.

The early morning peak in search rate that we observed also was reported for Madagascar Fish-Eagles by Razafindramanana (1995) and for Bald Eagles (Steenhof et al. 1980, Mersmann 1989) and Ospreys (*Pandion haliaetus*; Flemming and Smith 1990). This peak may result from hunger after fasting overnight or from eagles taking advantage of greater fish availability and calmer weather during the early morning hours. The early afternoon search rate peak may reflect eagles that have digested the morning food and are hungry again. Whitfield and Blaber (1978) observed

a midday foraging peak in African Fish-Eagles (*Haliaeetus vocifer*) and suggested that the eagles were taking advantage of thermals at this time, but the Madagascar Fish-Eagles that we observed foraged mostly low over the water from a perch. Daily weather patterns varied little during the study, so differences among eagle pairs in foraging rates and success probably were not related to weather.

Dietary preference.—The results suggest that Madagascar Fish-Eagles prefer *Ophicephalus striatus* to other fish and avoid *Cyprinus carpio*. *Ophicephalus striatus* was the largest fish species that we saw fish-eagles capture. We estimated the largest ones caught by fish-eagles to be between 1 and 1.5 kg. This species is a predatory fish that was introduced to Madagascar in 1978 (Reinthal and Stiassny 1991). In field experiments, Bald Eagles selected large fish more often than smaller fish during the breeding season, but not during the non-breeding season (Jenkins and Jackman 1995); Madagascar Fish-Eagle preference for *O. striatus* may reflect the eagle's greater energy requirements during the breeding season. Fish-eagles showed no preference for *Heterotis niloticus*, another large introduced fish species, but it was present in only three (33.3%) of the nine lakes. *Cyprinus carpio* may not be used because this species feeds on the bottom of lakes (Scott and Crossman 1973) where it is difficult for eagles to catch.

The results also may indicate biases in the fish abundance data. *Ophicephalus striatus*, a visually orienting predator, may be better at avoiding entanglement in gill nets than the other fish species. All of the *C. carpio* abundance data were from a single lake where we caught 33 individuals. This lake was so shallow (0.9 m) that both gill nets extended to the bottom and consequently were more likely to catch bottom-dwelling fish such as *C. carpio*.

The use and relative abundance data for tilapia, the most abundant fish in all of the lakes, were similar (64.7% of identifiable fish-eagle catch and 67.5% of gill net catch). Tilapia were introduced to Madagascar for aquaculture in the 1950s (Kiener 1963) and have since spread to most bodies of freshwater throughout the island. The predominance of tilapia in the fish-eagles' diet in this study suggests that the Madagascar Fish-Eagle is an opportunistic predator that catches whatever prey species are most abundant. Thus, the marked change in species composition of Madagascar's freshwater fish fauna resulting from exotic species introductions (Loiselle 1993, Reinthal et al. 1995) probably has not been detrimental to the island's fish-eagle population. The positive relationship between fish-eagle foraging success and number of fish species suggests that the fish-eagle population may be sensitive to declines in fish species diversity.

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